

An individual-based growth and competition model for coastal redwood forest restoration

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Abstract: Thinning treatments to accelerate coastal redwood forest stand development are in wide application, but managers have yet to identify prescriptions that might best promote *Sequoia sempervirens* (Lamb. ex D. Don) Endl. (redwood) growth. The creation of successful thinning prescriptions would be aided by identifying the underlying mechanisms governing how individual tree growth responds to competitive environments in coastal redwood forests. We created a spatially explicit individual-based model of tree competition and growth parameterized using surveys of upland redwood forests at Redwood National Park, California. We modeled competition for overstory trees (stems ≥ 20 cm stem diameter at breast height, 1.37 m (dbh)) as growth reductions arising from sizes, distances, and species identity of competitor trees. Our model explained up to half of the variation in individual tree growth, suggesting that neighborhood crowding is an important determinant of growth in this forest type. We used our model to simulate the effects of novel thinning prescriptions (e.g., 40% stand basal area removal) for redwood forest restoration, concluding that these treatments could lead to substantial growth releases, particularly for *S. sempervirens*. The results of this study, along with continued improvements to our model, will help to determine spacing and species composition that best encourage growth.

Key words: forest dynamics, *Sequoia sempervirens*, spatial pattern, tree growth.

Résumé : Les traitements d'éclaircie visant à accélérer le développement des peuplements de séquoia côtier (*Sequoia sempervirens* (Lamb. ex D. Don) Endl.) sont largement appliqués, mais les aménagistes n'ont pas encore identifié les modalités qui optimiseraient la croissance du séquoia. La mise au point de prescriptions adéquates serait facilitée par l'identification des mécanismes qui déterminent la réaction de croissance des arbres à leur environnement compétitif dans les forêts de séquoia côtier. Nous avons paramétré un modèle de croissance et de compétition spatialement explicite à l'échelle de l'arbre à partir d'inventaires de forêts bien drainées de séquoia du parc national de Séquoia en Californie. Nous avons modélisé la compétition des arbres dominants (arbres d'au moins 20 cm de DHP) en termes de réduction de croissance causée par des arbres concurrents selon leur taille, leur distance et leur espèce. Notre modèle explique jusqu'à 50 % de la variation de la croissance des arbres individuels, ce qui indique que la concurrence des arbres voisins est un facteur important de la croissance dans ce type forestier. Nous avons utilisé notre modèle pour simuler les effets de nouvelles modalités d'éclaircie (p. ex. : prélèvement de 40 % de la surface terrière du peuplement) pour restaurer les forêts de séquoia, ce qui nous a permis de conclure que ces traitements peuvent engendrer des réactions de croissance substantielles, particulièrement dans le cas de *S. sempervirens*. Les résultats de cette étude, de même que les améliorations continues apportées à notre modèle, devraient aider à déterminer l'espacement et la composition en espèces qui favorisent une meilleure croissance. [Traduit par la Rédaction]

Mots-clés : dynamique forestière, *Sequoia sempervirens*, patron spatial, croissance des arbres.

Introduction

A primary challenge in conserving coastal redwood ecosystems is the restoration of degraded forests. The need for action is clear: over 90% of coastal redwood forests have been logged (Sawyer et al. 2000a), and the typical structure of young redwood stands impedes the rapid recovery of old forest (old growth) conditions such as dominance of *Sequoia sempervirens* (Lamb. ex D. Don) Endl. (redwood), distinct canopy layers, and diverse understory vegetation (O'Hara et al. 2010; Teraoka and Keyes 2011). Young forests are commonly comprised of dense, even-aged *Pseudotsuga menziesii* (Mirb.) Franco (Douglas-fir) and *S. sempervirens* stump sprouts, with simple canopy structure and little understory development. Under these conditions, the relatively shade-intolerant *P. menziesii* is expected to exclude *S. sempervirens* from the upper canopy until large gaps are formed, a process that may take centuries (Thornburgh et al. 2000). Moreover, many of these young second-growth stands

are believed to be vulnerable to disturbance in the form of drought, disease, and fire.

The primary restoration tool in coastal redwood forests is thinning, where competing vegetation is removed to promote growth of residual trees (O'Hara et al. 2010). These methods have a long history of success in commercial and non-commercial settings (Bauhus et al. 2009; Busing and Garman 2002; Wenger 1984). Some early restoration thinning prescriptions in redwood forests used spatially uniform tree spacing (Chittick and Keyes 2007), which contrasts with the spatial arrangement of stems in old forests (Dagley 2008; van Mantgem and Stuart 2012). However, newer methods that encourage spatial heterogeneity such as variable-density thinning are being tested (O'Hara et al. 2010, 2012). While restoration thinning treatments in coastal redwood forests have generally improved at least some aspects of stand conditions (e.g., understory development), thinning has not always improved residual tree growth over the long-term (>10 years following treat-

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ment) (Chittick and Keyes 2007; Teraoka and Keyes 2011) or given a clear competitive advantage to *S. sempervirens* over *P. menziesii* (Plummer et al. 2012). With better information concerning how individual tree growth is increased by reducing competition, which is the underlying rationale for thinning treatments, managers may be able to design more effective thinning prescriptions.

Understanding how competition operates in coastal redwood forests depends on our ability to measure and integrate several complex ecological relationships. Levels of aboveground and belowground resources available for tree growth are contingent on the abundance, size, distance, and species identity of competing vegetation (Canham et al. 1999; Canham et al. 2004). To understand these interacting influences, we need to address several questions: (i) to what degree is tree growth density-dependent (in terms of abundance and size of neighboring trees); (ii) how rapidly do competitive effects between individual trees diminish with increasing distance; and (iii) what are the pair-wise competitive abilities of the common species of redwood forests (e.g., is *S. sempervirens* better able than *P. menziesii* to exploit resources created by thinning treatments?). We require a relatively sophisticated analytical approach to simultaneously model these observations.

Methods for accurately describing the relationship between competition and growth have been developed for individually based forest models that allow non-linear competitive interactions that incorporate the size, distance, and species identity of competing trees (Bugmann 2001; Pacala et al. 1996). These complex models appear to offer modest improvement over indices of competition that do not consider individual interactions and the spatial arrangement of competing trees (Boivin et al. 2010; Stadt et al. 2007). Given sufficient data, these methods allow us to describe the interactions that control tree responses to thinning treatments and to estimate their effects in novel situations. In this paper, we measure individual tree growth across a range of growing conditions in coastal redwood forests. We use these data to develop a spatially explicit model of crowding and growth to describe competitive interactions in coastal redwood forests and then use this model to estimate growth releases under hypothetical thinning prescriptions.

Methods

Study site

We surveyed sites with contrasting management histories in Redwood National Park, California. The region features a Mediterranean climate, with mild, rainy winters and cool, dry summers (Sawyer et al. 2000b). Annual mean temperatures are approximately 15 °C, with annual precipitation of about 1700 mm, mostly occurring as winter rain. Summer fog is common near the coast, moderating dry summer conditions. Soils are primarily derived from sandstone, mudstone, and schist. Historically, the dominance of *S. sempervirens* was aided by frequent low- to medium-intensity fire (Lorimer et al. 2009), but fire has been largely excluded in coastal redwood forests over the past 100 years.

Plot establishment

We sought to measure tree growth across a broad set of potential competitive environments. We sampled young forests with a recent history of logging, young forests that had undergone experimental thinning, and old forests with no history of logging. For the thinned sites, we wanted to capture long-term responses, so we surveyed stands that had >10 years to respond to thinning treatments. Two sites at Redwood National Park met this criterion, locally known as the Whiskey 40 and Holter Ridge sites (Fig. 1). In both sites, we measured thinned and adjacent un-

thinned sites; for the Whiskey 40 area, we also measured nearby old forests.

Whiskey 40 is a 16 ha area of young forest embedded within a larger area of old forest. The site was logged in 1963 and features extremely dense stands consisting of *P. menziesii*, *S. sempervirens* sprouts, and species that were seeded in the site following logging (*Picea sitchensis* (Bong.) Carrière (Sitka spruce) and *Chamaecyparis lawsoniana* (A. Murray) Parl. (Port-Orford cedar)). A 14 ha area was thinned in 1995, removing all trees ≤11.4 cm stem diameter at breast height (dbh, 1.37 m) and exotic conifers (*P. sitchensis* and *C. lawsoniana*) of all sizes, reducing stand basal area by roughly 30%. By 2002, however, stand basal area had returned to near pretreatment levels (~55 m²·ha⁻¹) (Teraoka and Keyes 2011).

The nearby Holter Ridge site was originally logged in the early 1950s (Chittick 2005; Chittick and Keyes 2007). In the fall and winter of 1978 and 1979, approximately 80 ha of young forest at Holter Ridge was experimentally thinned using a variety of thinning intensities (based on tree spacing, ranging from approximately 3–5 m between trees). In all treatments, *S. sempervirens* sprouts were targeted. These treatments resulted in an immediate reduction in basal area of approximately 20%–25%, but a follow-up survey showed that, by 2003, thinned and unthinned “control” areas had similar basal areas (~65 m²·ha⁻¹) without a clear competitive advantage of *S. sempervirens* over *P. menziesii*.

We established 50 m × 50 m plots at random locations within thinned and unthinned young forests at the Whiskey 40 and Holter Ridge sites (Table 1) to capture the maximum amount of variability among sites. We established one plot each in the thinned and unthinned areas at Whiskey 40. At Holter Ridge, we established one plot in the 3 m spacing treatment, one plot in the 5 m spacing treatment, and two plots in the unthinned area. Within the plots, all trees ≥20 cm dbh were mapped and measured in 2009 and 2010. Old-forest stand structure and growth were taken from six 1 ha plots near the Whiskey 40 stand, where individual trees ≥20 cm dbh were mapped and measured in 1995 and re-measured in 2010 (Table 1; Fig. 1) (for details see van Mantgem and Stuart 2012).

Growth measurements

We determined radial growth using increment cores within young forest sites, coring all trees within these plots that were >5 m from the plot boundary to reduce edge effects. Cores were mounted on a solid frame and finely sanded, and then ring-width was measured using a dissecting microscope and a sliding stage micrometer. We used ring-width data to determine average annual growth rate over the most recent 10-year interval, which omits the years immediately after thinning (the 5-year growth interval produces similar results). Cores were not cross-dated, and redwood is known to have inconsistent radial growth patterns, particularly in second-growth stands and in stem clumps (Waring and O'Hara 2006), so growth measurement errors are possible from our tree cores. We determined radial growth in the old forest plots from repeated stem diameter measurements in 1995 and 2010. It is possible that these two methods of calculating growth might yield variation unassociated with local competitive environments, but residual plots of linear models of growth and competitive environments did not suggest systematic differences between these approaches (Supplementary Fig. S1).¹

There were 52 instances of negative growth and 18 instances of unrealistically large radial growth (>15 mm·year⁻¹), which probably arose from stem diameter measurement error. We wished to remove observations of negative growth and what we believed to be unrealistically large positive growth rates, but we did not wish to bias our results in a positive direction by removing all negative

¹Supplementary material is available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/cjfr-2014-0143>.

Fig. 1. Location of the Whiskey 40 and Holter Ridge sites within young forests at Redwood National Park, California. The six plots in an upland old forest near Whiskey 40 are shown with open symbols.

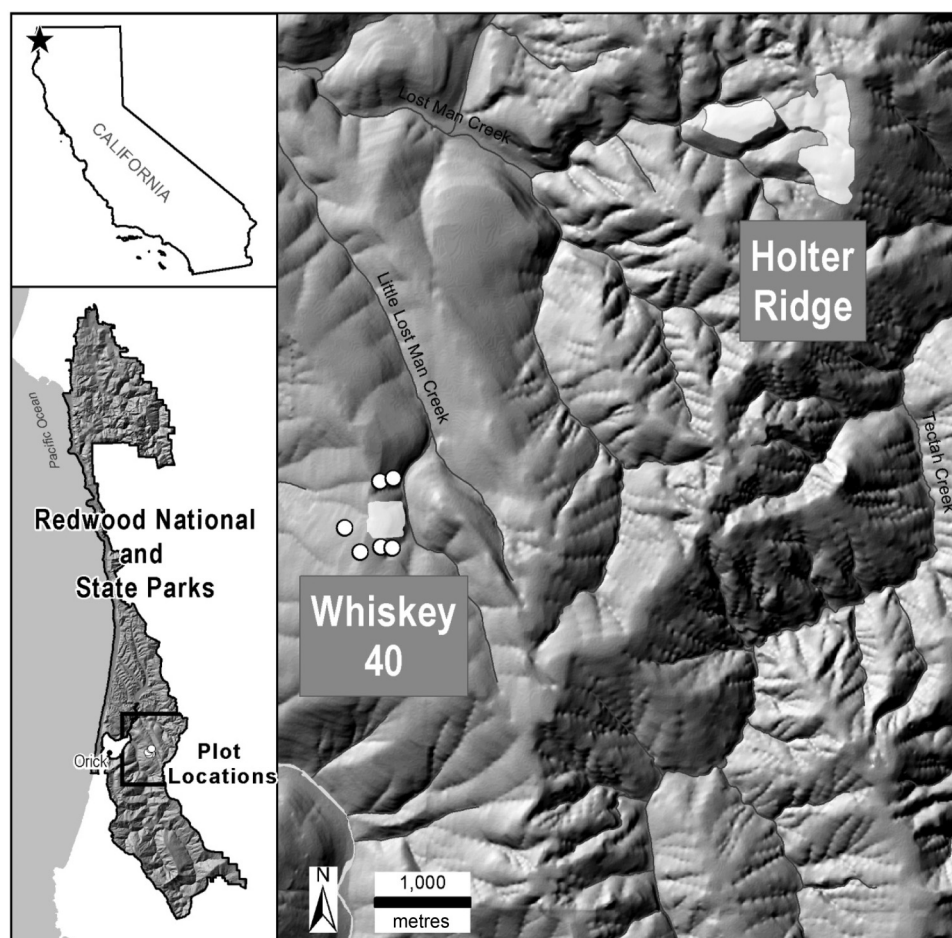


Table 1. Characteristics of forest plots (stems ≥ 20 cm dbh).

Treatment history	Plot	Site	Density (trees·ha ⁻¹)	Basal area* (m ² ·ha ⁻¹)	Species composition†
Young forest	1	Whiskey 40	668	48.1	SESE 39%, PSME 35%, TSHE 9%, LIDE 8%, PISI 6%, CHLA 4%
	2	Holter Ridge	712	70.0	PSME 62%, SESE 27%, TSHE 8%, LIDE 3%
	3	Holter Ridge	708	71.6	PSME 60%, SESE 29%, LIDE 10%
Young forest, thinned	1	Whiskey 40	744	49.0	PSME 53%, SESE 38%, LIDE 9%
	2	Holter Ridge	520	61.5	PSME 68%, SESE 25%, LIDE 6%, TSHE 1%
	3	Holter Ridge	448	74.2	SESE 51%, PSME 38%, LIDE 12%
Old forest	1	Whiskey 40	244	165.3	TSHE 46%, SESE 24%, PSME 16%, LIDE 13%
	2	Whiskey 40	175	175.9	TSHE 42%, SESE 27%, PSME 26%, LIDE 5%, ABGR 1%
	3	Whiskey 40	131	230.9	SESE 44%, ABGR 20%, TSHE 19%, PSME 9%, LIDE 7%, ARME 2%
	4	Whiskey 40	163	135.8	SESE 36%, LIDE 23%, ABGR 19%, TSHE 17%, PSME 5%
	5	Whiskey 40	193	145.6	LIDE 26%, SESE 25%, TSHE 25%, PSME 24%
	6	Whiskey 40	183	195.2	SESE 38%, TSHE 33%, PSME 25%, LIDE 3%

Note: ABGR, *Abies grandis*; ARME, *Arbutus menziesii*; CHLA, *Chrysopsis chrysophylla*; LIDE, *Notholithocarpus densiflorus* syn. *Lithocarpus densiflorus*; PISI, *Picea sitchensis*; PSME, *P. menziesii*; SESE, *S. sempervirens*; TSHE, *T. heterophylla*.

*High values for stand basal area due to presence of large *S. sempervirens*.

†Species composition $\geq 1\%$ of stem counts. Percentages may not add to 100 due to rounding.

growth rates (Condit et al. 2006). For this reason, we removed from the growth analyses stems that had radial growth rates less than -2 mm·year⁻¹ or greater than 15 mm·year⁻¹, approximately 2% of our observations. Retaining these observations gave qualitatively similar results.

To identify possible sampling biases arising from the selected study sites, we used linear mixed models (Gelman and Hill 2007) to identify differences in radial growth linked to management history (young forests, thinned young forests, and old forests)

while accounting for the effects of grouping by sampling location (study plot identity nested within the Whiskey 40 and Holter Ridge sites). Parameter estimates for management history were obtained using restricted maximum likelihood with confidence intervals (CI) created from 1000 bootstrapped samples. Mixed models were created using the lme4 package in R (R Core Team 2013; <http://www.r-project.org>). Conditional on the grouping variables, r^2 of the fitted models were calculated following Nakagawa and Schielzeth (2013) using the MuMIn package.

Growth-competition model

A primary rationale of thinning treatments is to reduce crowding, encouraging growth of the remaining trees. We modeled the effects of crowding on tree growth following the general procedures outlined in Canham et al. (2004), Uriarte et al. (2004), and Das (2012). We had sufficient samples to estimate the effects of crowding for *P. menziesii*, *S. sempervirens*, and *Tsuga heterophylla* (Raf.) Sarg. (western hemlock). Our approach modeled observed radial growth (RG) as an outcome of potential radial growth (PRG) of a “free growing” tree with reductions from competition (eq. 1):

$$(1) \quad RG = PRG \times \text{competition}$$

Lacking information on the light environment of individual trees, we considered competition only from crowding. Crowding was modeled as a function of the size and distance of neighboring trees, with the neighborhood crowding index of the focal tree (NCI) (eq. 2) written as

$$(2) \quad NCI = (\text{dbh}_{\text{focal}})^{\gamma} \sum_{i=1}^s \sum_{j=1}^n \lambda_i \frac{(\text{dbh}_{ij})^{\alpha}}{(d_{ij})^{\beta}}$$

where $\text{dbh}_{\text{focal}}$ is the diameter (cm) of the focal tree; dbh_{ij} is the diameter of the neighboring tree for $i = 1, \dots, s$ species and $j = 1, \dots, n$ neighbors of species s . The term d is the distance (m) of the neighboring tree ij , falling within the maximum neighborhood area (we estimated the neighborhood radii, parameter R , which was constrained to be between 5 and 20 across 0.5 m increments). Parameters α , β , and γ determine the shape of the response and are estimated from the data. Parameter α determines how crowding scales with the size of competing trees, parameter β estimates the effect of distance of the competitor tree, and parameter γ controls the influence of the size of the focal tree on crowding effects. We also considered a multiplier (λ) that allows for among-species differences in competitive abilities, ranging from 0 to 1. To reliably estimate species identity effects, we estimated λ only for those trees that had at least 100 pair-wise interactions. By this rule we estimated λ for *S. sempervirens*, *P. menziesii*, *Notholithocarpus densiflorus* (Hook. & Arn.) Manos, Cannon & Oh syn. *Lithocarpus densiflorus* (tanoak), and *T. heterophylla* (other minor species were assumed to have equivalent competitive strengths and were placed into a single group).

Competition was modeled to decline as a function of NCI (eq. 3):

$$(3) \quad \text{competition} = e^{-C \cdot \left(\frac{NCI}{NCI_{\text{max}}} \right)^D}$$

where C is a fitted parameter that determines how competition influences the rate of growth decline with NCI, with D describing the shape of the decline. If $D = 1$, the decline is a negative exponential function. If $D > 1$, the decline is sigmoidal. NCI_{max} is the maximum observed value of NCI. NCI was scaled to the maximum to facilitate comparisons of the C and D parameters among species.

We tested several model forms associating PRG to tree size (see Supplementary material)¹ but found the following simple power function to adequately describe this relationship:

$$(4) \quad PRG = a \cdot \text{dbh}^b$$

where a and b are fitted parameters. Models using different formulations of the relationship between PRG and tree size were compared using Akaike's information criterion (AIC) (Burnham and Anderson 2002) and Bayesian information criterion (BIC), as AIC can be biased to favor complex models (Link and Barker 2010)

(Supplementary Table S1).¹ Estimates for parameters a and b , relating measurements of growth to the size of the focal tree, generally suggested linear relationships regardless of model form (Supplementary Table S2).¹

We estimated parameters using maximum likelihood and simulated annealing, using the likelihood package in R (http://www.sortie-nd.org/lme/lme_R_code_tutorials.html). Parameter estimate uncertainty was calculated as two unit support intervals, roughly equivalent to a 95% support limit. We also calculated the r^2 of a linear regression of observed versus predicted values as an additional measure of fit.

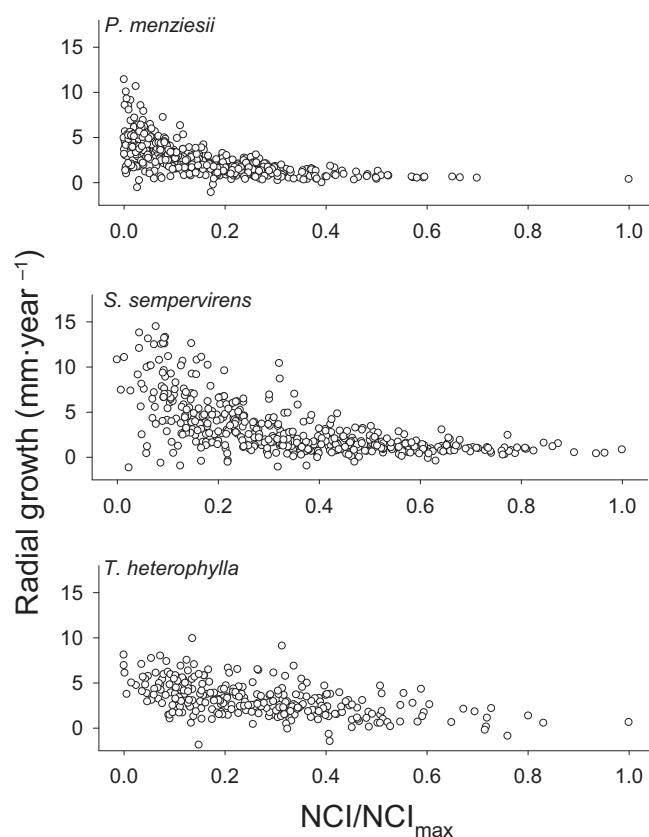
To evaluate the potential effects of alternate thinning treatments, we simulated thinning treatments based on newly developed prescriptions in use at Redwood National Park (U.S. National Park Service 2008), though they have been deployed too recently to assess long-term outcomes. There are two primary prescriptions: (i) moderate-intensity, where 40% stand basal area is removed without targeting particular size classes; and (ii) low-intensity, where 25% stand basal area is removed, targeting canopy dominants and co-dominants (thinning from above). Both prescriptions call for the preferential removal of *P. menziesii*. We simulated these prescriptions in our unthinned young forests by randomly removing individual *P. menziesii*, followed by other species (excluding *S. sempervirens*), until basal area targets were met. For the “thinning from above” simulation, we removed trees in the largest quantile of the stem size distribution until the basal area target was met. We then estimated the expected growth given the simulated stand conditions using our modeled relationships between crowding and growth.

Results

Our study plots measured a relatively wide range of stand conditions, with sample plots typically containing higher stem densities and lower basal areas in young versus old forest plots (Table 1). That is, our sampling plots in young forests typically contained large numbers of small trees relative to our sampling plots in old forests. There was no readily apparent difference in density and basal area between thinned and unthinned young forest plots or across thinning treatments at the Whiskey 40 and Holter Ridge sites. Linear mixed models suggested that average radial increment was lower in young versus old forests, with no noticeable differences between the thinned and unthinned young forests (relative to old forests; thinned = -1.95 , 95% CI = -3.12 to -0.79 ; unthinned = -2.17 , 95% CI = -3.34 to -0.94). However, mixed models predicting growth using stand history accounted for only a small amount of additional variation over a null model without treatment history (stand history conditional $r^2 = 0.231$, null conditional $r^2 = 0.230$). These results imply that local competitive environments were the dominant influence on individual tree growth, rather than unexplained differences due to past management of these stands.

We found NCI and tree size to be strong predictors of individual tree growth (*P. menziesii* $r^2 = 0.49$, *S. sempervirens* $r^2 = 0.50$, *T. heterophylla* $r^2 = 0.39$; Supplementary Table S1).¹ Growth declined sharply with increasing crowding for all species (Fig. 2), with *P. menziesii* being the most sensitive to crowding. All species showed an exponential decline in growth with increasing crowding (parameter $D \approx 1$) (Table 2). Effective neighborhood distances (parameter R) varied slightly among species, ranging from 11.5 to 14.5 m. Parameter α for *S. sempervirens* was near 1, suggesting that competition scaled linearly with the diameter of competing trees. For *P. menziesii* and *T. heterophylla*, parameter α was near 2, so that competition scales linearly with the basal area of competing trees. The estimated values for parameter β show that for *P. menziesii*, the effect of a competitor tree is strongly determined by its distance, whereas for *S. sempervirens* and *T. heterophylla*, the distance of the competitor tree was much less important so long as it was

Fig. 2. Observed radial growth for common species relative to crowding, as calculated by relative NCI (see eq. 2 in the text).



within the effective neighborhood distance. Finally, our estimates of parameter γ suggest that the effects of competition decline with increasing focal tree size for all species but most strongly for *P. menziesii*.

The competitive hierarchies estimated by parameter λ suggest that *T. heterophylla* is a strong competitor, particularly for *S. sempervirens* (Fig. 3). Surprisingly, *P. menziesii* is relatively insensitive to *T. heterophylla* but is more strongly affected by *L. densiflorus* and intraspecific competition. Competitive hierarchies for *S. sempervirens* suggest that this species is a relatively weak competitor against commonly co-occurring species.

Simulations suggested improved growth under both moderate- and low-intensity thinning treatments for *S. sempervirens*. Moderate-intensity thinning reduced local competitive environments, resulting in significant improvements in expected radial growth compared with expected growth without thinning (median Δ expected radial growth = 0.08 mm·year⁻¹, $P < 0.0001$, paired permutation test) (Fig. 4). Low-intensity thinning resulted in smaller, but still significant, expected growth releases (median Δ radial growth = 0.05 mm·year⁻¹, $P < 0.0001$, paired permutation test). We obtained similar results for *P. menziesii* (moderate-intensity thinning median Δ radial growth = 0.07 mm·year⁻¹, $P < 0.0001$, paired permutation test; low-intensity thinning, median Δ radial growth = 0.03 mm·year⁻¹, $P < 0.0001$, paired permutation test). Both thinning treatments appear to allow greater expected growth releases in *S. sempervirens* compared with *P. menziesii* ($P < 0.01$, two-sample permutation tests). There were too few observations of *T. heterophylla* in the young forests to model growth responses from increased thinning intensities.

Discussion

Our models of tree growth in coastal redwood forests demonstrated that local crowding has a large influence on tree growth, as has been found in other forest types (Canham et al. 2004; Uriarte et al. 2004). While our model could be improved with supplemental data such as light competition or site conditions, it accounts for a relatively large proportion (approximately 40%–50%) of the variation observed in tree growth. These models underscore the complexity of growth responses to crowding, which vary non-linearly with tree size, competitor tree size and distance, and species identity of both focal and competitor tree.

Our model supports the view that the spatial arrangement of residual trees is a key determinant of growth following thinning (Churchill et al. 2013). Improved growth of residual trees following thinning is often an important restoration goal, along with other metrics of stand structure such as understory diversity (Chittick and Keyes 2007; Teraoka and Keyes 2011). If relatively uncrowded areas are needed for long-term increases in growth (e.g., changes that persist >10 years following treatments), then thinning prescriptions that call for uniform tree spacing would likely need to be relatively aggressive (i.e., remove a large number of trees or a large proportion of stand basal area). In contrast, variable-density thinning, in which patches of low and high tree density are created, could be used to produce neighborhoods of both low and high crowding while removing fewer trees. Early results (4 years after thinning) from variable-density thinning experiments in coastal redwood forests have resulted in substantial growth in residual trees (O'Hara et al. 2010). Stand structure following variable-density thinning may also better mimic the clumped spatial arrangement of stems in old coastal redwood forests (Dagley 2008; van Mantgem and Stuart 2012). Thinning via prescribed fire may also create or maintain spatial heterogeneity (van Mantgem et al. 2011), but its effectiveness has yet to be tested in coastal redwood forests.

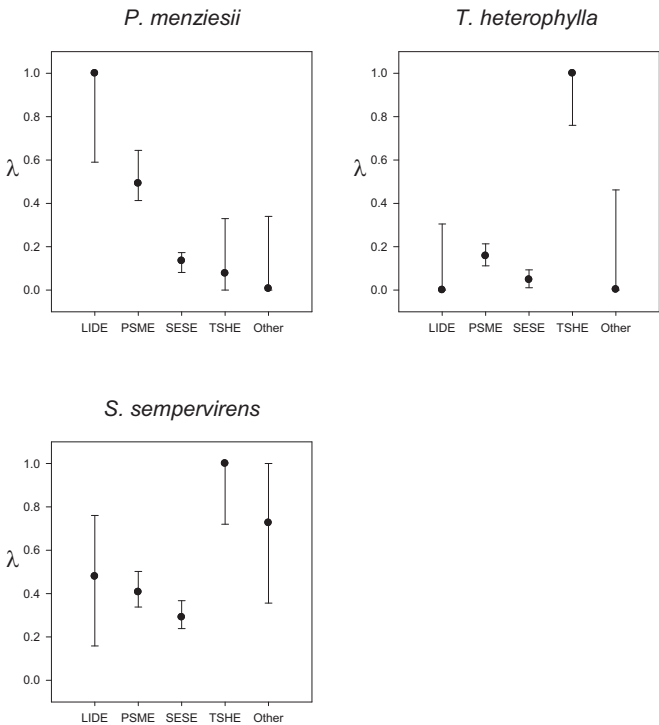
Our model of local competition and growth offers insights into the design of thinning treatments to encourage growth of *S. sempervirens*. First, *S. sempervirens* appears to respond more favorably to aggressive thinning than does *P. menziesii*. This lends support to thinning prescriptions designed to favor *S. sempervirens* over *P. menziesii* using the removal of a substantial portion of stand basal area (e.g., up to 40% of basal area) or thinning overstory *P. menziesii*. Second, *S. sempervirens* was found to be relatively resistant to competition, though it did not appear to be a strong competitor against *P. menziesii* or *T. heterophylla*. This suggests that *S. sempervirens* will be able to maintain growth, and potentially persist, even under relatively crowded conditions. That is, in agreement with earlier assessments of coastal redwood forest stand development (Teraoka and Keyes 2011), it appears likely that unthinned areas will maintain populations of *S. sempervirens* but may not recover dominance of this species in the near future. Third, the estimated effective neighborhood distance for *S. sempervirens* was large (up to 14.3 m), with competitive effects declining only slightly with distance from the focal tree within this neighborhood. This suggests that thinning could occur over relatively large neighborhoods (i.e., thinning occurring up to a 14 m radius) to achieve growth releases for *S. sempervirens*. Lastly, the effect of *P. menziesii* on the growth of *S. sempervirens* ($\lambda \approx 0.4$) was not strong relative to other species, so that the preferential removal of *P. menziesii* in thinning treatments may result in less *S. sempervirens* growth relative to the removal of other species. However, there are relatively few other species available for removal in young forests, and maintaining species diversity will likely be a more important management consideration than simply increasing *S. sempervirens* growth.

Of course, an important issue that still needs to be addressed is how well our models transfer from one redwood stand to another and ultimately how accurate they might be on a more regional scale. There is no a priori reason to expect our stands to be unique

Table 2. Competition parameter estimate (expressed as mean with range in parentheses) for the simple power function model. Parameter *C* determines how competition influences the rate of growth decline with the neighborhood competition (or crowding) index (NCI), with *D* describing the shape of the decline (see eq. 3 in the text). Parameters α , β , and γ determine the shape of the response of the focal tree to crowding, determining NCI (see eq. 2 in the text). Parameter *R* is the estimated maximum neighborhood area.

	<i>C</i>	<i>D</i>	α	β	γ	<i>R</i>
<i>P. menziesii</i>	2.50 (2.35–2.58)	1.00 (1–1.05)	2.35 (2.33–2.4)	2.35 (2.33–2.4)	–1.95 (–2.05–1.8)	14.50 (13.8–14.65)
<i>S. sempervirens</i>	2.08 (1.99–2.16)	1.00 (1–1.06)	1.10 (1.03–1.13)	0.35 (0.26–0.45)	–0.62 (–0.75–0.55)	14.31 (14.31–14.74)
<i>T. heterophylla</i>	1.90 (1.69–2.06)	1.03 (1–1.13)	1.74 (1.51–1.99)	0.79 (0.69–0.89)	–0.30 (–0.54–0.16)	11.50 (10.84–11.73)

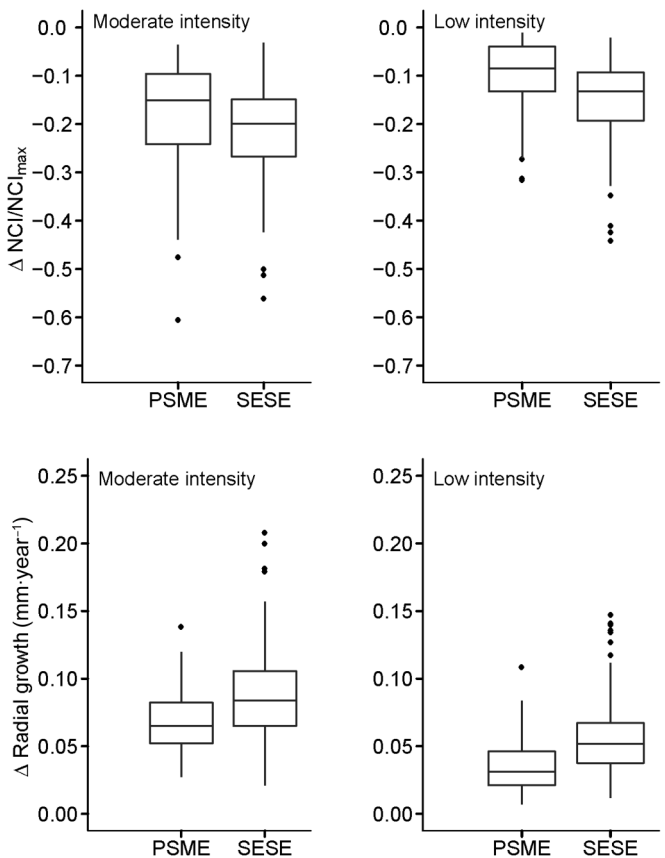
Fig. 3. Relative competitive strengths as estimated by parameter λ (eq. 2) for common species in upland redwood forests. LIDE, *Notholithocarpus densiflorus* syn. *Lithocarpus densiflorus*; PSME, *Pseudotsuga menziesii*; SESE, *Sequoia sempervirens*; TSHE, *Tsuga heterophylla*; Other, other minor species.



regionally but, as with any empirical model, we encourage rigorous testing across a wider landscape to refine and verify the approach.

Testing these results will depend on a commitment to repeatedly measure the effects of thinning treatments. While it is clear that reducing competition via thinning can increase the growth of residual trees, we are still uncertain what an optimal level of thinning might be, how thinning intensities should vary under different site conditions (e.g., stand slope, aspect, and age), how treatment effects may change as stands mature and, as noted above, how competitive processes might vary across the landscape. In some cases, it may be possible to thin stands a second time (second-entry thinning), but this is often difficult due to funding constraints and the removal of roads following restoration treatments (Madej et al. 2013). Restoring young forests is a key component of coastal redwood forest conservation, not only to accelerate the development of old forest structure, but also to enhance forest resilience to disturbance. Though it is still unclear if thinning treatments will confer resilience to disturbance in coastal redwood forests, observations from other forest types are promising (D'Amato et al. 2013; Fulé et al. 2012). This presumed benefit from restoration thinning may become an increasingly important consideration in an era of climate change.

Fig. 4. Modeled reductions in relative NCI and radial growth increases from hypothetical thinning treatments, relative to unthinned stands. Hypothetical thinning treatments were based on prescriptions from Redwood National Park: moderate-intensity thinning removed 40% stand basal area; low-intensity thinning removed 25% basal area from dominant and co-dominant trees. Both treatments preferentially removed *P. menziesii*. Species codes follow Fig. 3.



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